Complex mortuary dynamics in the Upper Paleolithic of the decorated Grotte de Cussac, France

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The Mid-Upper Paleolithic (Gravettian) karstic Grotte de Cussac (France) contains two areas of human remains in the context of abundant (and spectacular) parietal engravings. The first area (loci 1 and 2) includes the skeleton of a young adult male in a bear nest, rearranged by postdecomposition inundation, and the variably fragmentary remains of at least two individuals distributed across two bear nests, sorted anatomically and with most of the elements constrained to one side of one nest. The second area (locus 3) retains remains of two adults and an adolescent, in upper hollows and variably distributed down the slope, largely segregated into upper versus lower body groups. The only decoration associated with the human remains is red pigment on some of the bones or underlying sediment. The human remains indicate variable nonnatural deposition and manipulation of human bodies, body portions, and skeletal elements of at least six individuals. Moreover, Cussac is unusual in the association of these remains with exceptional parietal art. The complex Cussac mortuary pattern joins growing evidence from other Gravettian sites of variable treatment of individuals after death, within and across sites, in terms of formal deposition of the body versus postmortem manipulation versus surface abandonment. It provides a window onto the social diversity and the complex interactions of the living and the dead among these successful Late Pleistocene foragers.

Paleolithic foragers | funerary behaviors | archeothanatology | decorated cave

The Mid-Upper Paleolithic of Europe (Gravettian *sensu lato*; ~35,000 to ~25,000 y ago) is well known for large open-air and rockshelter sites, diverse and sophisticated subsistence, cave paintings, human (especially female) figurines, body decoration, and variably elaborate burials (1). The last aspect has received particular attention, given that mortuary behaviors are closely associated with diverse social customs in ethnographic contexts and should provide a window onto such behaviors in the past (2, 3). The Gravettian formal burials include neonates to older adults, single and multiple individuals, varying numbers of beads (from a few to thousands), different levels of ochre application (from localized to full body), occasional mobiliary art or other forms of grave goods, and an abundance of biologically unusual individuals (4–7). These remains are known from open air sites (in central and eastern Europe) and rockshelters/cave entrances (in southern and western Europe). There are several cases of apparent human manipulation of the remains, and a number of the sites (with and without burials) have yielded isolated human remains apparently from individuals not receiving formal burial.

These Gravettian burials, combined with other aspects of the Mid-Upper Paleolithic, provide an image of these populations as "Hunters of the Golden Age" (1). They suggest a high point in sociocultural elaboration prior to the environmental deterioration of the Last Glacial Maximum. In this context we describe an additional set of Gravettian mortuary remains from the decorated Grotte de Cussac in southwestern France. They provide further evidence for mortuary practices beyond primary burial, as well as a setting for the dead that is unique for the Paleolithic.

Results

The Grotte de Cussac. The Grotte de Cussac (Le Buisson-de-Cadouin, Dordogne, France) consists of a single, subhorizontal karstic tube, ancient meanders of an underground river with a succession of sinuous passages and low or raised passages that sometimes cut the meanders (8). It is separated into two branches from the present entrance: one ~1.0 km long to the southeast and one 0.6 km long to the northwest (Fig. 1). Discovered in 2000, Cussac revealed associated parietal art, prehistoric surfaces, and human remains (9). It was designated a national heritage site and remains closed to visitors. All research observations are noninvasive and restricted to a single path through the karstic tube in order to protect all traces of human and faunal activity. Hence, any analysis is restricted to remote observations of the remains and to the study of photographs and three-dimensional (3D) photogrammetric models, both limited by available lumination, extensive viewing distances for some of the remains, and bones partially or totally covered with cave sediment (*SI Appendix*). The cave has nonetheless been studied since 2010 under the

Significance

Gravettian mortuary practices provide a key perspective on social complexity during the Upper Paleolithic. Such inferences have been drawn mostly from the formal burials relatively abundant for this period. Here we present the bioanthropological study of Grotte de Cussac, a decorated cave with Gravettian human remains deposited on the floor. These bone accumulations correspond to several forms of deposition (a whole body, body parts on the surface, and dry bones in bear nests), plus displacement and removal of elements that indicate diverse and complex mortuary behaviors. The exceptional preservation during millennia of these surficial deposits illustrates steps of a mortuary landscape that are beyond reach in more usual Upper Paleolithic burial sites.

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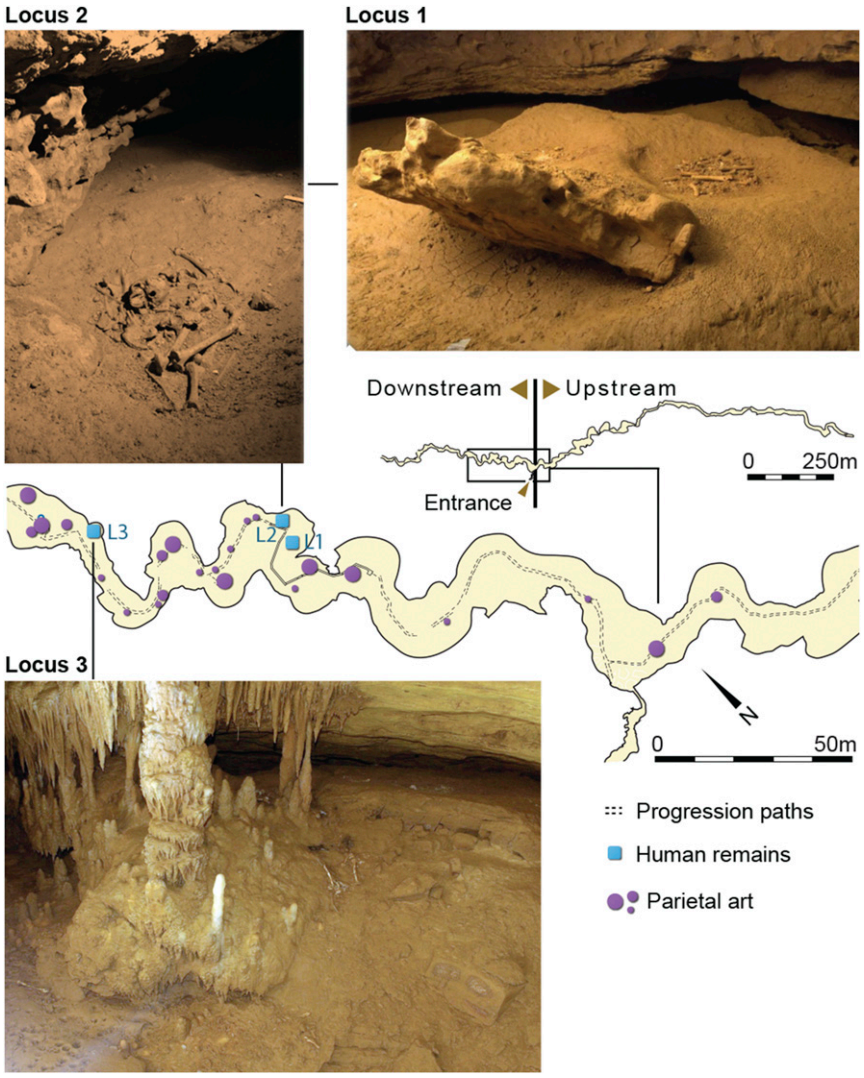

Fig. 1. General view of the loci with human remains and their locations in the karstic network of the Grotte de Cussac. Karstic system drawing: François Lacrampe-Cuyaubère (graphic artist, PCR Cussac). Loci 1 and 2 are located in the same area, ~150 m from the cave entrance, while locus 3 is situated 80 m deeper in the cave.

direction of J. Jaubert, and the contribution here is a portion of the larger ongoing project.

Tracks and claw marks on the floor and walls of the cave, as well as numerous bear hibernation nests, demonstrate that bears frequented the cavity before any human incursions (10). Other evidence of animals are few, including rare animal bones (from small carnivores, cattle, rabbits, and birds), some of which were close to the entrance and may have been introduced by small carnivores (8). Human activity is evident first and foremost by the presence of rock art along the entire karstic network. Except for a few nonfigurative elements (mainly dots) made in black or red paint, the art consists of deep engravings into the limestone. More than 800 engravings are known, mainly figurative representations of animals (notably bison, mammoths, bovines, and horses), as well as human representations including stylistic female silhouettes and male and female genitalia (8, 11). Other evidence of human activity includes several preserved footprints (10) and torch marks on the walls along the path, plus three lithic artifacts and a worked reindeer antler (8). Finally, there are two main areas that contain human remains in the downstream branch of the cave (8, 12). All of these traces of prehistoric human activity indicate deep karst activity and appropriation (8, 10, 11, 13).

The human activity in Cussac was initially attributed to the Gravettian, primarily based on the art (8, 9), which displays features typical of the Middle Gravettian style and similarities with the parietal art of Quercy and the Pyrenees. This chronological attribution is confirmed by two ^{14}C dates [each with a calibrated 95.4% probability interval, computed with OxCal 4.2, and using IntCal 13 (14)]: one on charcoal from the cave floor (25,150 ± 210 B.P.; 29,704 to 28,714 cal B.P.; GifA-13150) and one on a human rib fragment from locus 1 depression 2 (25,120 ± 120 B.P.; 29,500 to 28,835 cal B.P.; Beta-156643). The dates also suggest the contemporaneity of the human remains and parietal art (8).

The Human Remains. The Cussac human remains occur in two areas (Fig. 1). The first area (loci 1 and 2), ~150 m from the cave entrance, consists of bones and/or teeth in and near three shallow bear hibernation nests. The second area (locus 3), 80 m deeper in the cave, includes bones in shallow depressions high along the cave wall and dispersed down the slope below. In addition, there are scattered isolated bones on the surface around

these primary clusters. No human remains have been located elsewhere in the cave system. There are no faunal remains (such as bear bones) in the vicinities of the human remains. A laminar flake was found on the path near locus 1.

Loci 1 and 2. Loci 1 and 2 are to the east of the path (Fig. 1), with a few large blocks of fallen limestone and several depressions, three of which are bear nests (Fig. 2*A* and *SI Appendix*). The surface of these loci consists of fine-grained sediment, due to Late Pleistocene inundation of its lower elevations. There are three main bone accumulations, all in bear nests.

The largest bear nest, locus 2 depression 1 (L2-D1), contains ≥47 disarticulated, largely complete, and excellently preserved skeletal elements that can all be attributed to one adult male (15, 16) (*SI Appendix*). Almost all visible bones are covered by a sediment layer, deposited from several flooding events (8) (Fig. 2*B* and *SI Appendix*). The disarticulation and rearrangement of the bones from their original anatomical positions (limited movement of the largest and heaviest elements, significant displacement or absence of the smallest and most trabecular bones) is most parsimoniously viewed as the product of flotation after full decomposition of a body deposited in a prone position (12, 15, 16). To the extent determinable, given the in situ position and sediment covering, none of the major skeletal elements were removed.

In contrast, locus 1 depression 2 (L1-D2) is a clearly circumscribed 70-cm diameter accumulation of human bones and osseous debris at the bottom of 1-m diameter bear hibernation nest (Fig. 2*C*). The inferred stratigraphy of the skeletal deposit is: 1) the floor of the bear nest overlaid by 2) a thin red pigment layer, then 3) a bed of fragmentary bones mixed with sediment, topped by 4) larger and more intact bones. The entire accumulation is vertically thin, most of the bones are surficially evident, and none are covered with alluvial sediment. None of the remains are in anatomical position in situ, and except for a few small compact elements (tali, phalanges, and some vertebrae), all of the bones are incomplete. Seventy-eight skeletal elements bigger than 5 mm are evident, 63 are identifiable as bone, especially major long-bone diaphyseal sections, vertebrae, unfused epiphyses, small manual and pedal bones, a fragmented mandible, and four isolated mandibular teeth that likely derive from the mandible. Conspicuously absent are cranial and pelvic remains and maxillary teeth. Based on the tali and femoral shaft diameters, as well as on the presence of unfused epiphyses and exposed long-bone metaphyses, there are at least two individuals, one adult and one early-to-middle adolescent (*SI Appendix*).

The bone cluster is located against one side of the bear nest, and there is a broad area within the nest and around the cluster that contains neither bones nor osseous debris; the human bones are therefore distinctly bounded. The depression is above the maximum inundation level (8); therefore, there is no evidence of biotic or abiotic disturbances that could explain the circumscription of the disarticulated broken bones. The pattern therefore cannot be the product solely of the deposition and decomposition of intact bodies, given the absence of some elements and the constrained diameter of the osseous cluster. It might represent the placement of bodies or body segments within the depression, followed by decay, natural compaction, and

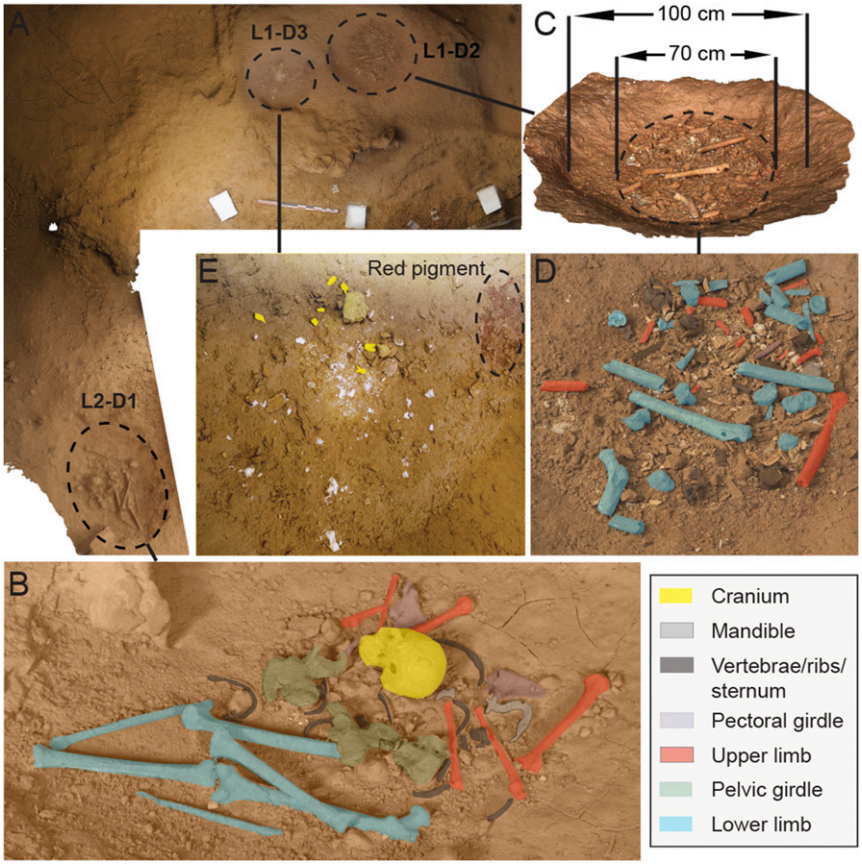

Fig. 2. (*A*) Orthoplane rendition of loci 1 and 2. (*B*) Skeletal elements of one individual in the L2-D1 bear nest. (*C*) Clearly circumscribed accumulation of human bones in the L1-D2 bear nest. (*D*) L1-D2 bone cluster with larger bones highlighted. (*E*) L1-D3 with seven maxillary teeth and an area of red pigment highlighted.

postmortem manipulation. However, the under-representation of vertebrae and small distal limb bones makes more likely a scenario of an anthropic deposition of skeletal elements from bodies that decomposed elsewhere (i.e., a secondary burial). The bounded nature of the accumulation (Fig. 2*C*) suggests that the bones were carefully placed within the depression, possibly in a perishable container.

The adjacent locus 1 depression 3 (L1-D3) bear nest contains six maxillary teeth from an adolescent and one tooth from an adult (Fig. 2*D* and *SI Appendix*). The teeth are clustered around small pieces of limestone and white powder, possibly deriving from degraded bone. The adolescent's dental age (12 to 14 y) corresponds well with the epiphyseal maturation of the L1-D2 adolescent and the wear of the mature tooth is compatible with the L1-D2 mandible. It is likely that the teeth in L1-D3 represent the sole remains of isolated crania. Because L1-D3 is above the line of maximum inundation (8), the original cranial elements were not naturally displaced to the depression. They must have been deposited there after separation from their vertebrae and mandibles. Given the otherwise abundant bone preservation in the depressions, the crania were probably removed subsequent to alveolar degeneration, thus suggesting at least two stages of bone manipulation.

Outside these depressions in the loci 1 and 2 area, there are nine isolated human bones. Some of them are embedded in sediment and thus appear to have been displaced by water, most likely from L2-D1, whereas the agent explaining their final location is not clear for the other bones. One of those bones, a left patella found near the path in 2001, retains red pigment (*SI Appendix*).

Locus 3. Locus 3 is a larger area to the east of the passage (Fig. 1), consisting of small clusters of bones in depressions around the upper portion of a large stalagmitic mass and more elements variably isolated or clustered down the slopes around the stalagmites (Fig. 3*A*). The distribution of the latter bones is best viewed as an original deposition of human remains on the top of the slope, followed by downslope movement of the elements. Locus 3 exhibits 103 skeletal elements from a late adolescent and two adults based on the number of right humeri (9, 17) (*SI Appendix*).

On the (difficult to visually access) upper level, there are two main clusters of human remains. The L3-D1 cluster, north of the stalagmitic mass, is a well-circumscribed, 60-cm diameter accumulation of surficial bones (not embedded) in a bear nest (Fig. 3*B* and *SI Appendix*). Traces of red pigment are apparent on the bottom and edges of the depression under a thin layer of brown sediment (Fig. 3*B*). The 13 variably fragmented identifiable bone elements all derive from the lower body, from the lumbar region to the posterior tarsals. Based on size, these bone elements are from at least two adult individuals. The condyles of two femora and one femoral head retain calcite incrustations (Fig. 3*B*), indicating that they were displaced from a previous location. This observation, as well as that of the constrained surface of the bone cluster and the absence of small elements of the midfoot and forefoot, suggest that the bone accumulation is unlikely the product of in situ decomposition of intact bodies and later disturbance or human manipulation. As with L1-D2 and L1-D3, the L3-D1 cluster should be the product of the deposition of skeletal elements from bodies that decomposed elsewhere.

The second main cluster (L3-TS [top slope]), to the south of the stalagmites, includes two vertebrae and a rib, plus the long bones of a right upper limb, a scapula, and 11 hand bones (the last in anatomical connection) possibly from the same upper limb (Fig. 3*C*). The degrees of long-bone epiphyseal fusion suggest a late adolescent (16 to 21 y) (*SI Appendix*). All of these bones are partially embedded in sediment.

A few additional bones, most of them extremely fragmented, are present on the upper level in several remote clusters. They include a femoral fragment and the distal half of a right humerus, at least two isolated teeth (but no apparent cranial or mandibular elements), and a few unidentifiable skeletal fragments.

Other human remains are visible at intervals down the L3 slope (L3-DS), below the partial upper limb (Fig. 3*D*). They include upper limb and axial remains and two pieces of (probably one) mandible, but no evidence of cranial, pelvic, or lower limb remains. The long bones are aligned with the slope, and the bones at the bottom are largely embedded. This suggests sediment creep from the upper level, due to gravity associated with the water-saturated sediment. Below the main slope, there are additional elements variably on the surface or covered, including upper limb long bones, vertebrae, and ribs. One of those bones, a right ulna, retains red pigment.

Based on several lines of evidence (see ref. 17 and above), locus 3 contains at least three individuals, including one late adolescent and two adults (*SI Appendix*). The adolescent is represented by a nearly complete right upper limb (on the top of the slope), possibly a distal fragment of a left humerus (below the slope), a fragment of a very small coxal bone (in L3-D1), and mandibular fragments (in the slope) retaining a partially erupted left third molar. One of the adults is represented by the long bones of right and left upper limbs scattered along and below the slope and possibly a right fibula (in L3-D1). The third individual is represented only by a complete right humerus.

Overall, locus 3 is notable for having complete bones or a major section of bones, few foot bones, and bones crushed in situ only in the upper left depression. There is also a separation of upper and lower limb elements, although vertebrae are variably present throughout. Crania are absent, which cannot be attributed to the apparent movement of remains down the slope considering the excellent preservation of the bones in that area. This also holds for the separation of upper versus lower limb remains, since downslope movement should be determined by size and geometry but not by limb. In order to explain these

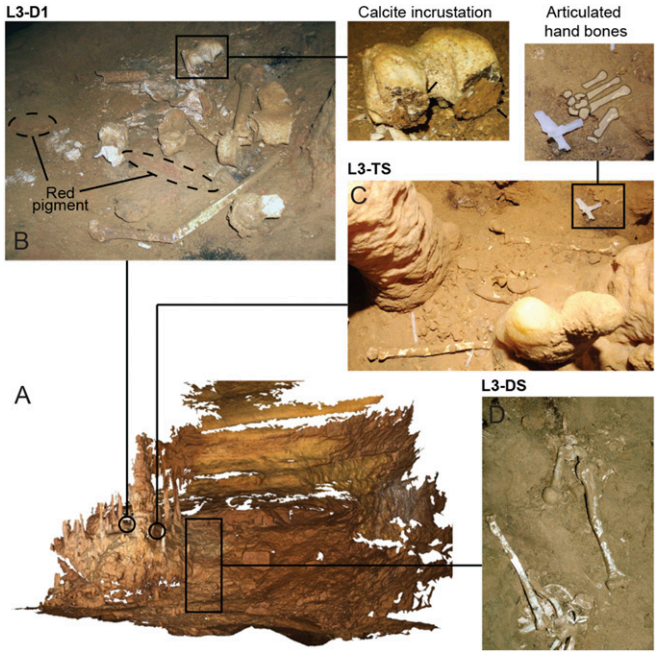

Fig. 3. (*A*) Global 3D model of the locus 3. (*B*) L3-D1 circumscribed accumulation of lower body bones of two or more individuals with traces of red pigment. (*C*) L3-TS with primarily right upper limb bones. (*D*) Single bone accumulations visible down the L3-DS slope.

aspects, some form of manipulation of body parts or skeletal elements, before or after their deposition in locus 3, should have been involved.

Interlocus Associations and Minimum Number of Individuals. The human bone accumulations from Cussac therefore include the following: 1) the remains of an apparently complete adult skeleton in the locus 2 bear nest; 2) partial remains of a younger adolescent mixed into the L1-D2 bone cluster and represented by several teeth in L1-D3; 3) very incomplete remains of an adult in the L1-D2 cluster and possibly represented by one tooth in L1-D3; 4) various remains (especially mandible and upper limb bones) of a late adolescent in locus 3; and 5) segregated upper limb versus lower limb remains of at least two adults clustered or scattered across locus 3. Although the remains of two individuals can be associated across L1-D2 and L1-D3, it is not possible to draw any interloci anatomical connections. Given the virtual completeness of the skeleton in locus 2 (Fig. 2), that individual is separate from the other loci. In addition, the upper limb long bones of the adolescent in L1-D2 precludes any connection with the L3 adolescent, and the same appears to apply to the L1-D2 adult and the two adults from locus 3. The most likely scenario therefore is that the L2-D1, L1-D2 + L1-D3, and L3 represent separate depositions of human remains. Combined with skeletal maturation and the number of right humeri, the minimum number of individuals for the Grotte de Cussac is six.

Discussion

There are several lines of evidence that point toward deliberate deposits of human bodies, body parts, and/or bones in the Grotte de Cussac. Some of these lines make Cussac similar to other Gravettian sites, whereas others are unique in the Gravettian funerary landscape.

Cussac is the first location where the human remains were deposited deep in a decorated cave. All previously known Gravettian formal burials are located in open air sites, rockshelters, or cave entrances. A possible exception is Vilhonneur (southwestern France), where a partial skeleton of a young adult was discovered in a cave with parietal art but without clear association with that art (18).

The deposition of bodies or body parts on the floor (instead of in a grave) was relatively common in the Gravettian of southwestern France; it has been identified or inferred at Cussac, Cro-Magnon, Abri Pataud, Vilhonneur, and Gargas, whereas graves are absent in this area (12, 18–20). It is rare elsewhere, having been identified only at Sunghir (Russia) and Pavlov I (Czech Republic), sites that also yielded elaborate burials (21, 22).

At Cussac, almost all of the human remains are located in bear nests, a previously undocumented depositional context for the Gravettian. This could be an intention to enclose the human remains in bounded features in a manner analogous to deposition in a burial pit. This analogy is reinforced by the use of red pigment (L1-D2/D-3 and several places in L3), which is found in most Gravettian burials (5–7). However, none of the individuals at Cussac were apparently associated with body decoration, whereas beads are ubiquitous in Gravettian burials (if variable in quantity) (4–7).

Three forms of deposition are recognized within Cussac: a whole body in a bear nest in L2, body parts on the surface of a platform above L3, and dry bones in bear nests (L1-D2, L1-D3, and L3-D1). The virtually complete skeleton in L2-D1 indicates that primary deposition of a body happened at least once at Cussac. The body was also placed in a prone position, which is uncommon during the Gravettian, with only three other occurrences known: BT3 in Baousso da Torre (Italy), GE5 in the Grotte-des-Enfants double burial (Italy), and DV14 in the Dolní Věstonice II triple burial (Czech Republic) (5, 7). The other Cussac bone accumulations are somewhat organized, thus suggesting that they are intentional deposits, made as parts of distinct mortuary behaviors. There was also some intentional selection of skeletal elements during this process, which is evidenced by the separation of upper and lower limb bones in L3 and the absence of cranial remains in all secondary deposits. The isolated maxillary teeth (L1-D3) indicate removal of crania and hence that postmortem manipulation took place inside the cave. The lack of five crania of six suggests that this occurred repeatedly. The other bone accumulations are clearly the result of postmortem manipulation, although the timing and locations of these manipulations are less clear. For example, the nearly complete L3 adolescent right skeletal upper limb in partial articulation may indicate the introduction of a body portion inside the cave or, alternatively, the removal of the other elements after deposition of an intact body and its decay. Another example is the accumulation of bones in L1-D2, which implies the deposit of dry bones in a circumscribed area, possibly using a perishable container.

Such diversity of deposition within a single site is rare but does exist in the Gravettian. At Sunghir, four of the individuals were intentionally buried, two more had their remains manipulated, and one seems to have received little or no formal treatment (21). These three forms of disposal are also apparent at the Dolní Věstonice/Pavlov site complex (22, 23). At Abri Pataud, the whole bodies of infants were apparently deposited, whereas body parts of adults were deposited and/or removed (19). Finally, at Buran-Kaya III (Crimea), Fournol (France), and El Castillo Cave (Spain), fragmented human remains, some of them displaying cut marks, are known (24–26). However, two types of manipulations at Cussac are unknown elsewhere for the Gravettian: the removal of crania and the deliberate commingling of the remains of several individuals.

The Cussac sample is composed of teenagers and adults with no evidence of infant or juvenile remains. This demographic profile is not uncommon for the Gravettian, but it is for southwestern France, where infants and children are relatively abundant (19, 26, 27). Cussac L2A displays an unusually small body size and limb proportions, as well as unusual skull morphology, for a Gravettian male (15, 16) (*SI Appendix*). Both his burial and the apparent absence of postmortem manipulation may reflect special social status (28). However, developmental anomalies and abnormalities are abundant in the Gravettian buried sample (and throughout the Pleistocene) (29), and the meaning of the burials of individuals, with abnormalities that would have been evident to their kin, remains unclear.

There are few instances where Gravettian human remains were found close to parietal art (Abri Pataud, Paglicci, Gargas, Vilhonneur, El Castillo, Arene Candide), but without strict associations in terms of contemporaneity and symbolic value. At Cussac, the contemporaneity of the mortuary rites and the art is highly likely considering the very homogeneous artistic style in the cave and the virtually identical ^{14}C dates for a human bone and a charcoal sample (8). Even if the people who manipulated the human remains may not have been the same as the artists, it seems impossible, considering the path used during the Gravettian, that the art or the human remains were ignored when the other took place.

The association of mortuary rites and art raises the question of the social meaning of the deposit of bodies, associated with postmortem manipulation, in this decorated cave. A recent analysis of the Grotte de Cussac Grand Panel intermingled engravings concluded that it was likely the result of a collective image-making performance implying performer(s) and an audience and that the collective role given to these visual productions was actively integrated into past social networks as a medium for information exchanges to negotiate social identity (11). We therefore suggest that the mortuary behaviors at Cussac participated in a similar way in a social network requiring long-term

transmissions of values (30). The temporary relocation of the person in a liminal space (bear nests in the cave) after death, the loss of individuality after decomposition through the commingling the bones of several individuals, and finally the reincorporation of remains through the removal of crania evoke patterns of mortuary behavior that have been variously described in the ethnographic record as "rites of separation and incorporation" (31–33). These may have been used to reaffirm and negotiate individual and group identity among the living (31–33). This interpretation, frequently formulated for more recent archaeological groups (34, 35), would place the Grotte de Cussac as the oldest example of a global spirituality encompassing deep karst occupation, art manifestations, and the dead and the living.

Conclusion

The diverse positions, skeletal part representations, and variable commingling of human remains in the Mid-Upper Paleolithic Grotte de Cussac, alongside abundant parietal engravings, deep within the Cussac karstic system, provide an additional window onto the Gravettian funerary landscape. In addition to the well-known and often elaborate burials of this time period, the mortuary evidence from Cussac and other sites is an indication of a complex social landscape in which there was differential treatment of individuals after death in terms of burial versus surface deposition of their remains, postmortem manipulation of bodies and body portions, and the locations of their final resting places. Cussac mortuary remains are therefore providing a window, beyond the evidence of successful hunter-gatherer adaptations and abundant art, into the social dynamism of these Late Pleistocene early modern humans.

Materials and Methods

This analysis of the Cussac human remains is based on the original bones and their contexts, which remain in situ in the Grotte de Cussac. Observations come from visual observation, photographic assessment, and 3D renderings of the three loci (all details are provided in *SI Appendix*). The 3D renderings were initially generated using our custom photogrammetric solutions based on the Bundler and PMVS programs (36, 37) and, since 2014, on Photoscan (Agisoft). Three-dimensional models were scaled using a local scale, and reference points taken with a total station. Meshing was done with 3D Systems software.

Data Availability. The primary data consist of the identifications of the human skeletal elements in the Grotte de Cussac and their distributions in the three loci. These data are all in *SI Appendix*, Tables S1–S9 and in *SI Appendix*, Figs. S6–S13, as well as in the text and Figs. 1–3. Additional data on the skeletal immaturity of elements from loci 1 and 3 are in *SI Appendix*, Tables S10–S12.

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